

# EARLY PALEOCENE (PUERCAN AND TORREJONIAN) ARCHAIC UNGULATES (CONDYLARTHRA, PROCREODI AND ACREODI) OF THE SAN JUAN BASIN, NEW MEXICO

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**Abstract**—We present the first comprehensive revision of all San Juan Basin Paleocene archaic ungulates, which are known from fossils collected primarily on BLM-administered lands. A brief description is given of each species of archaic ungulate found in the Puercan and Torrejonian strata of San Juan Basin. The description includes holotype information, revised diagnosis and distribution information. Taxonomic status, temporal ranges of archaic ungulate species and their importance for biostratigraphy are discussed in detail.

## INTRODUCTION

The San Juan Basin, New Mexico, has produced more Paleocene mammalian fossils than any other location in North America. Most of these fossils come from BLM-administered lands. Many articles have been published on different groups of Paleocene vertebrates from this area, but surprisingly there were very few comprehensive studies of San Juan Basin Paleocene mammalian faunas. The only comprehensive detailed revision of San Juan Basin Paleocene mammals was undertaken by William D. Matthew (1937). Williamson and Lucas (1992, 1993) described the Paleocene biostratigraphy and vertebrate paleontology of the San Juan Basin. Williamson (1996) studied the geology of the Nacimiento Formation of San Juan Basin and briefly discussed its mammalian fauna, placing it into a detailed biostratigraphic framework. We present a comprehensive revision of all San Juan Basin Paleocene archaic ungulates and briefly discuss their biostratigraphic distribution.

**Institutional abbreviations:** AMNH = American Museum of Natural History, New York; KUVF = University of Kansas, Museum of Vertebrate Paleontology, Lawrence; NMMNH = New Mexico Museum of Natural History, Albuquerque; UCMP = University of California, Museum of Paleontology, Berkeley; USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C. **Other abbreviations:** P – upper premolars; M – upper molars; p – lower premolars, m – lower molars.

## SYSTEMATIC PALEONTOLOGY

### ORDER PROCREODI MATTHEW, 1909

#### Family Arctocyonidae Giebel, 1855

#### Subfamily Arctocyoninae Giebel, 1855

#### *Arctocyon ferox* (Cope, 1883)

Figs. 1, 2

**Lectotype**—AMNH 3268, right m2.

**Diagnosis**—A species of *Arctocyon* that differs from *A. corrugatus* by its larger size (15–20%) and from *A. acrogenius* by its smaller size (25%); also differs from *A. corrugatus* by its more robust lower jaw and shorter postorbital constriction.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico (Nacimiento Formation) and Montana (Lebo Formation).

**Comments**—Taxonomy of North American species of *Arctocyon* was discussed in detail by Kondrashov and Lucas (2004).

#### *Arctocyon corrugatus* (COPE, 1883)

Fig. 3

**Holotype**—AMNH 3258, right maxillary fragment with P4–M3.

**Revised diagnosis**—Smallest North American *Arctocyon*: 15–

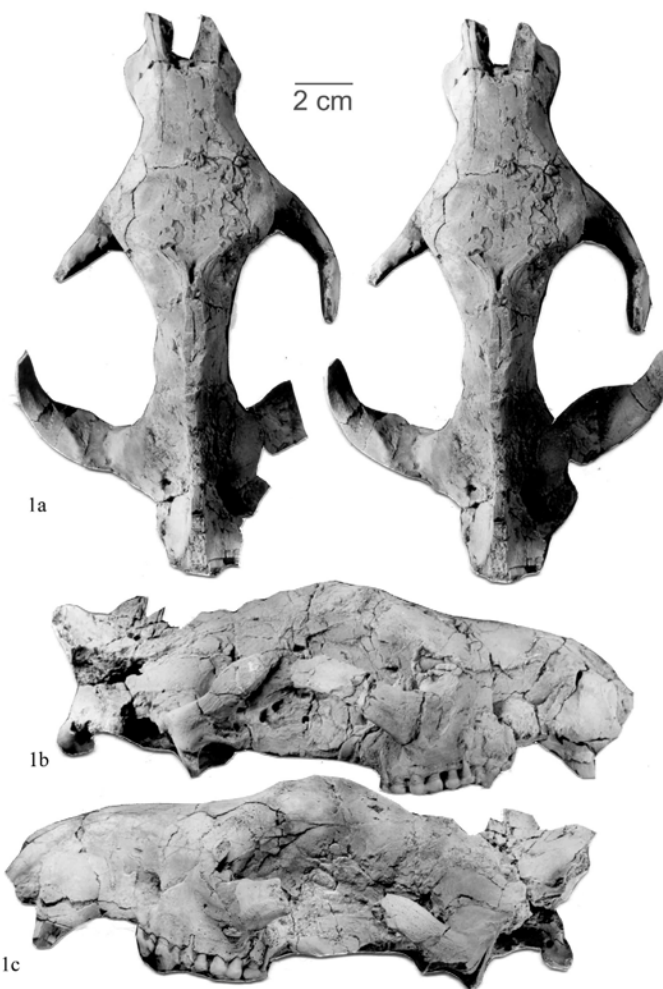


FIGURE 1. Skull of *Arctocyon ferox*, NMMNH P-8627, dorsal stereophotograph (a), right lateral (b) and left lateral (c) views.

20% smaller than *A. ferox* and 40% smaller than *A. acrogenius*.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico and Paleocene (Torrejonian–Tiffanian) of Montana.

#### *Colpoclaenus procyonoides* (Matthew, 1937)

**Holotype**—AMNH 16554, left maxillary fragment with P1–M3, left dentary fragment with c, p4–m3.

**Diagnosis**—Differs from *C. silberlingi* and *C. keeferi* in having a

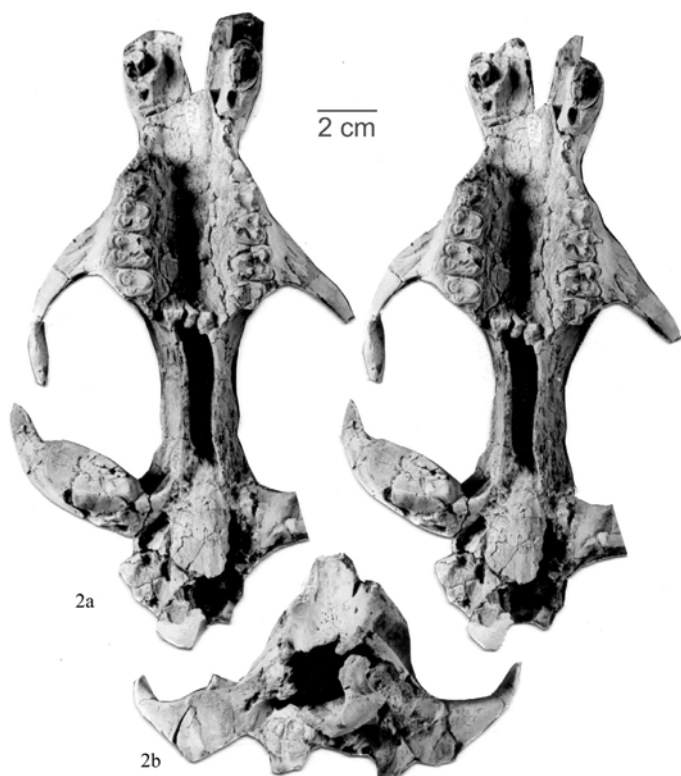


FIGURE 2. Skull of *Arctocyon ferox*, NMMNH P-8627, ventral stereophotograph (a) and occipital view (b).



FIGURE 3. *Arctocyon corrugatus*, AMNH 3258 (holotype), right P4-M3, occlusal view (a); USNM 407535, right mandibular fragment with p4-m3, occlusal view (b).

relatively well-developed M1-2 hypocone. Also differs from the other two species in being smaller.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico and Wyoming.

#### Subfamily Chriacinae Osborn et Earle, 1895

##### *Chriacus pelvidens* (Cope, 1881)

#### Fig. 4

**Holotype**—AMNH 3097, left dentary fragment with p4-m3.

**Diagnosis**—Differs from *Ch. baldwini* and *Ch. badgleyi* in being larger. Also differs from *Ch. badgleyi* in having better-developed conules and hypocone, in having a more molarized p4 with a metaconid and by the presence of a hypoconulid on m1. Differs from *Ch. orthogonius* in having rounded subtriangular upper molars. Differs from *Ch. gallinae* in having very well developed, complete upper molar cingula.

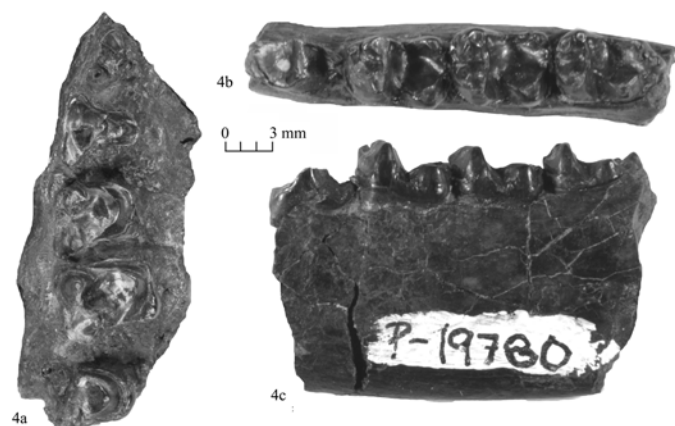


FIGURE 4. *Chriacus pelvidens*, KUPV 9519, right maxillary fragment with P4-M3, occlusal view (a); NMMNH 19780, left mandibular fragment with p4-m3, occlusal (b) and labial (c) views.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico and Wyoming.

##### *Chriacus baldwini* (Cope, 1882)

#### Fig. 5

**Holotype**—AMNH 3114, left dentary fragment with dp2-4.

**Diagnosis**—Slightly smaller than *Ch. pelvidens*, but larger than *Ch. badgleyi*. Differs from *Ch. orthogonius* in having rounded subtriangular upper molars. Differs from *Ch. gallinae* in having very well developed cingulum on upper molars.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico, Montana, Utah and Wyoming.

**Comments**—Van Valen (1978) described *Ch. calenancus* and differentiated it from *Ch. baldwini* in having a “more vertical posterior

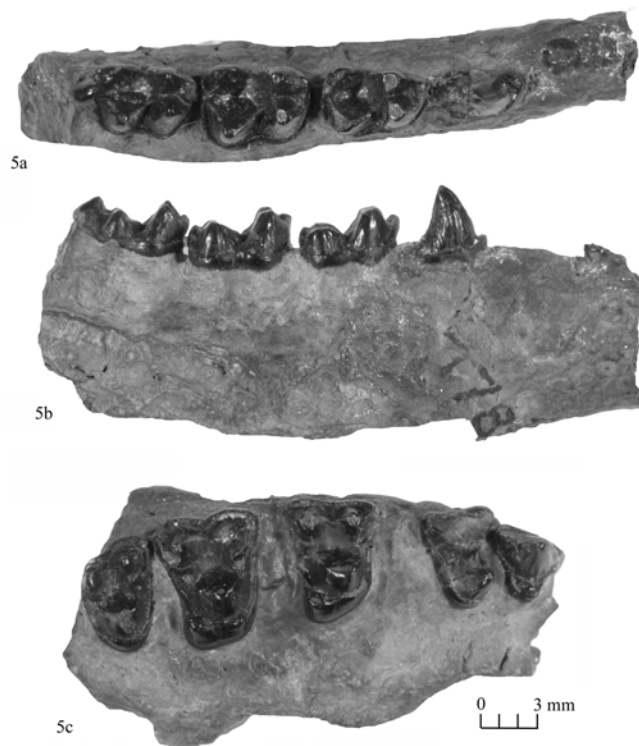


FIGURE 5. *Chriacus baldwini*, KUPV 7787, right dentary fragment with p4-m3, occlusal (a) and labial (b) views; KUPV 9519, right maxillary fragment with P3-M3, occlusal view (c).

trigonid wall and smaller entoconid." Existing intraspecific variation of lower teeth of *Ch. baldwini* does not support the integrity of *Ch. calenancus*, so we consider it a junior subjective synonym of *Ch. baldwini*. Williamson (1996) suggested that *Ch. calenancus* is a subspecies of *Ch. baldwini*.

***Prothryptacodon ambiguus* (Van Valen, 1967)**

**Holotype**—AMNH 16591, left dentary fragment with c, p4, m2, right humerus, one lumbar and three caudal vertebrae.

**Diagnosis**—Differs from *P. furens* and *P. yalensis* in being 20% smaller and in having a shorter p4 protoconid.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico, Wyoming and Canada.

**Comment**—Van Valen (1967) initially referred this species to a new genus *Pantinomia*, which he tentatively placed in Pantolestidae. Van Valen (1978) later synonymized *Pantinomia* and *Prothryptacodon* and so referred *P. ambigua* to Arctocyonidae. Fox (1968) described *Prothryptacodon albertensis* from the early Paleocene of Canada. Van Valen (1978) placed this species in *Oxyprimus* and synonymized *P. albertensis* and *Carcinodon aquilonius* Russell, 1974. The synonymy was later questioned by Johnston and Fox (1984), who also suggested that *P. albertensis* should be placed in *Prothryptacodon*. After Van Valen (1978) referred *Pantinomia ambigua* to *Prothryptacodon*, *P. albertensis* became inseparable from *P. ambiguus*, which was described a year earlier, and so has priority. Rigby (1980) described *Prothryptacodon* cf. *P. furens* from Wyoming, which is identical to *P. ambiguus* in size and morphology.

**Subfamily Oxyclaeninae Scott, 1892**

**Tribe Oxyclaenini Scott, 1892**

***Oxyclaenus cuspidatus* (Cope, 1884)**

**Fig. 6**

**Lectotype**—AMNH 3252, left maxillary fragment with P4-M3.

**Diagnosis**—A species of *Oxyclaenus* that differs from *O. simplex* in weak development of the M1-2 hypocone, lingually projecting M2 parastyle and larger size (15-20%). Differs from *O. antiquus* in being much smaller (30%).

**Distribution**—Lower Paleocene (Puercan) of New Mexico and Wyoming.

**Comment**—Van Valen (1978) mentioned that the type specimen is atypical, but it is within the range of intraspecific variability of this species. We restrict the holotype of *O. cuspidatus* to a maxillary fragment with P4-M3. Williamson and Carr (2004) suggested that the holotype specimen of *Oxyclaenus cuspidatus* belongs to *Microclaenodon*, which might alter the taxonomy of oxyclaenid arctocyonids if documented.

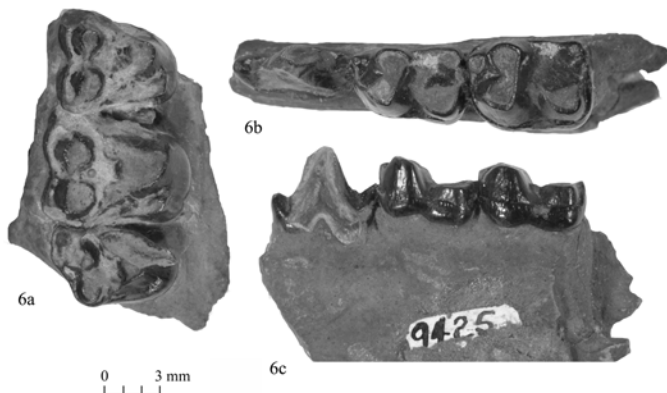


FIGURE 6. *Oxyclaenus cuspidatus*, KU 9435, right maxillary fragment with m1-3, occlusal view (a); KU 9425, left dentary fragment with p4-m2, occlusal (b) and labial (c) views.

***Oxyclaenus simplex* (Cope, 1884)**

**Fig. 7**

**Lectotype**—AMNH 3107, right maxillary fragment with M1-3.

**Diagnosis**—A small species of *Oxyclaenus* that differs from *O. cuspidatus* in having a more developed cingulum on M1-2 and being smaller (15-20%). Differs from *O. antiquus* in being much smaller (40-45%).

**Distribution**—Lower Paleocene (Puercan) of North America.

**Comment**—Van Valen (1978) synonymized *Carcinodon filholianus* Cope, 1884 with *O. simplex*; this synonymy was later questioned by Johnston and Fox (1984), but Williamson (1996) concluded that it was justified and we concur.

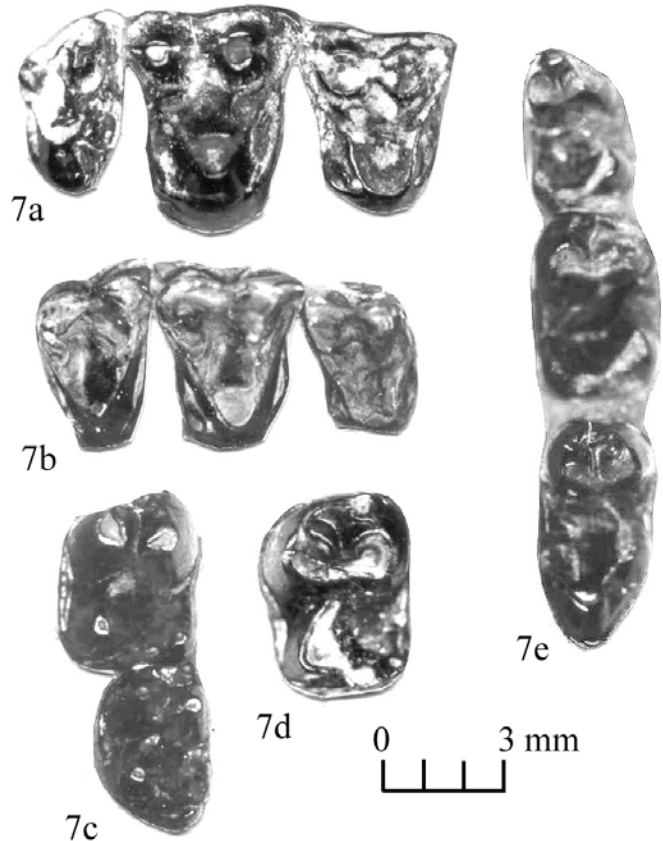


FIGURE 7. *Oxyclaenus simplex*, AMNH 3107, right M1-3 (*O. simplex* lectotype), occlusal view (a); AMNH 16415, right M1-3, occlusal view (b); AMNH 16347, left m2-3, occlusal view (c); AMNH 3107, left m2, occlusal view (d); AMNH 3205, right m1-3 ("*Carcinodon filholianus*" holotype), occlusal view (e).

***Oxyclaenus antiquus* (Simpson, 1936)**

**Fig. 8**

**Holotype**—AMNH 27714, maxillary fragment with P3-M3.

**Diagnosis**—The largest species of *Oxyclaenus*; larger than *O. cuspidatus* (30%) and *O. simplex* (45%).

**Distribution**—Lower Paleocene (Puercan) of the San Juan Basin, New Mexico.

**Comments**—Simpson (1936) described this species as *Chriacus antiquus* and Van Valen and Sloan (1965) assigned it to *Oxyclaenus*. Later, Van Valen (1978), following E. Manning's opinion (collection notes), referred this species to the genus *Baioconodon*. Williamson (1996) referred the species to *Oxyclaenus*. This species is almost identical in tooth morphology to *O. cuspidatus* but differs in its much larger size, so we agree with Williamson and treat *O. antiquus* as the largest species of the genus *Oxyclaenus*.

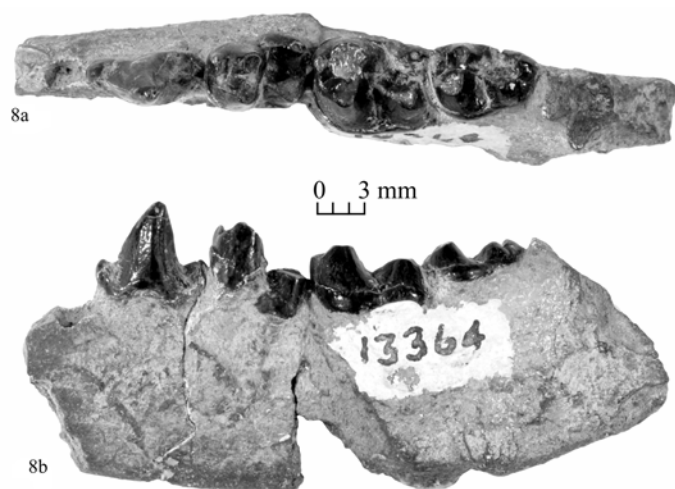


FIGURE 8. *Oxyclaenus antiquus*, KUVP 13364, left dentary fragment with p4-m3, occlusal (a) and labial (b) views.

**Tribe Loxolophini Van Valen, 1978**

***Loxolophus hyattianus* (Cope, 1885)**

**Fig. 9**

**Holotype**—AMNH 3121, left maxillary fragment with M1-3.

**Diagnosis**—The smallest species of *Loxolophus*; also differs from *L. priscus* in having relatively narrower lower molars, a considerably reduced m3 and an anteriorly-projecting m1 paraconid, shifted medially. Differs from *L. pentacus* in its much smaller size.

**Distribution**—Lower Paleocene (Puercan) of New Mexico and Wyoming.

***Loxolophus priscus* (Cope, 1888)**

**Fig. 10**

**Holotype**—AMNH 3108, incomplete skull with left P3-M3, right M2-M3 and dentary fragment with m1-2.

**Diagnosis**—Slightly larger than *L. hyattianus* and has relatively broader lower molars. Also differs from *L. hyattianus* in having an unreduced m3 and in the lingual position of the m1 paraconid. Differs from *L. pentacus* in being significantly smaller.

**Distribution**—Lower Paleocene (Puercan-Torrejonian) of New Mexico, Montana, Utah and Wyoming.

***Loxolophus pentacus* (Cope, 1888)**

**Fig. 11**

**Holotype**—AMNH 3192, right dentary with p2-m3.

**Diagnosis**—Species of *Loxolophus* that differs from both *L. hyattianus* and *L. priscus* in being significantly larger.

**Distribution**—Lower Paleocene (Puercan) of New Mexico and Wyoming.

***Tricentes subtrigonus* (Cope, 1881)**

**Fig. 12**

**Holotype**—AMNH 3227, skull fragment with right P4-M2.

**Diagnosis**—Morphologically similar to *Loxolophus*, differs in having three premolars, in its more reduced, centrally placed lower molar paraconids and in its less robust dentition.

**Distribution**—Early Paleocene (Torrejonian) of New Mexico.

**Comment**—Van Valen (1978) placed *Tricentes subtrigonus* in *Mimotricentes* and synonymized the two genera. The diagnosis of *Mimotricentes* clearly indicated that its representatives have four premolars (Simpson, 1935, 1937) instead of three in *Tricentes* (the basis of the generic name). Van Valen (1978) indicated that the Montana sample is polymorphic in this character. We failed to find the variation in number

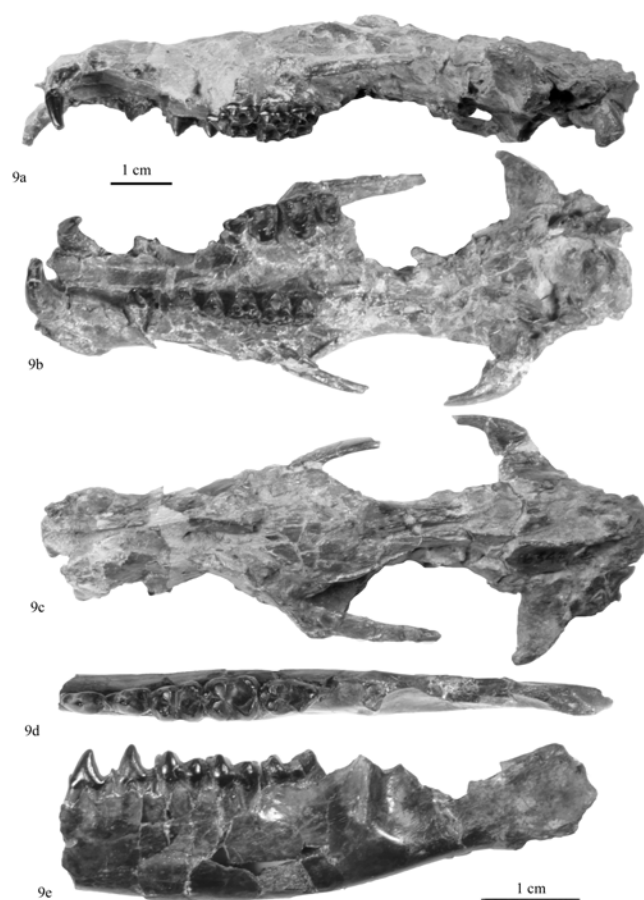


FIGURE 9. *Loxolophus hyattianus*, AMNH 16343: skull, lateral (a), ventral (b) and dorsal (c) views; left dentary with p3-m3, occlusal (d) and labial (e) views.

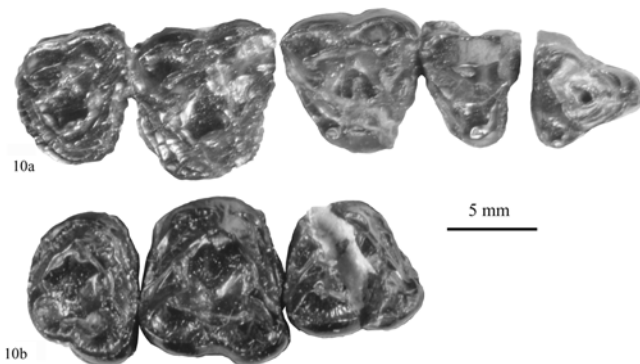


FIGURE 10. *Loxolophus priscus*, AMNH 3108, left P3-M3, occlusal view (a), right M1-3, occlusal view (b).

of premolars in the San Juan Basin sample, so we refer all New Mexico specimens to *Tricentes subtrigonus* and restrict *Mimotricentes* to the Fort Union sample.

***Desmatoclaenus protogonoides* (Cope, 1882)**

**Fig. 13**

**Holotype**—AMNH 3253, maxillary fragments with left and right M2-3.

**Diagnosis**—Differs from *D. diana* and *D. mearae* in having a weaker hypocone and parastyle; also differs from *D. hermaeus* in having a lingually-placed M2 hypocone and being smaller.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.



FIGURE 11. *Loxolophus pentacus*, AMNH 3192, right dentary with p3-m3 (holotype), occlusal (a) and labial (b) views.

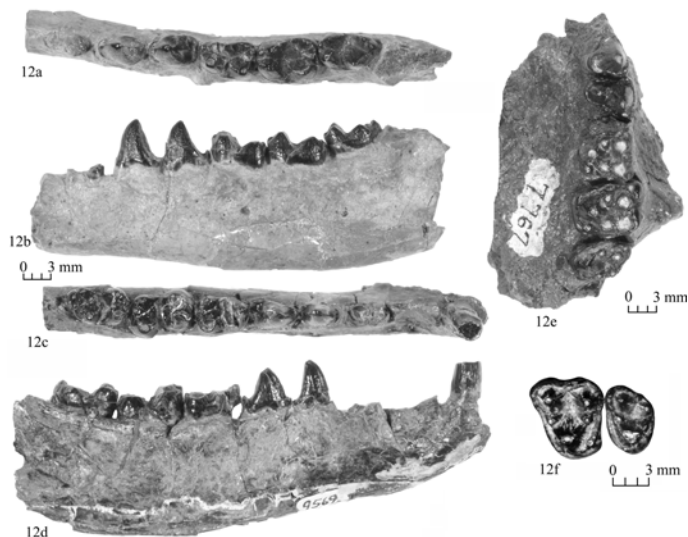


FIGURE 12. *Tricentes subtrigonus*, KUV 9569, left mandibular fragment with p3-m3, occlusal (a) and labial (b) views; KUV 7755, right mandibular fragment with p3-m3, occlusal (c) and labial (d) views; KUV 7767, left maxillary fragment with P3-M3, occlusal view (e); NMNH 16372, left M2-3, occlusal view (f).

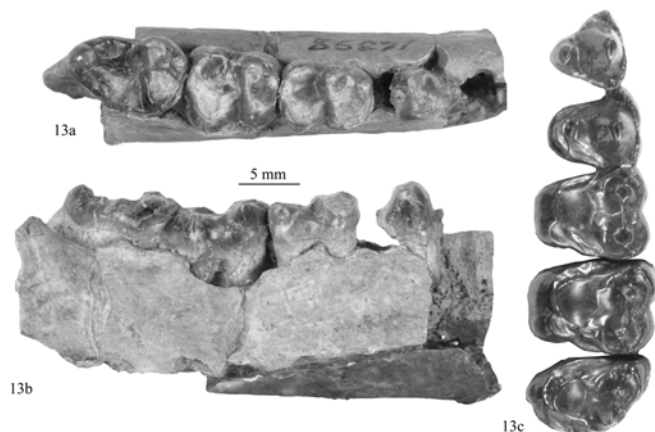


FIGURE 13. *Desmatoclaenus protogonoides*, AMNH 16398, right dentary fragment with p4-m3, occlusal (a) and labial (b) views; AMNH 16396, left P3-M3, occlusal view (c).

#### *Desmatoclaenus diana* Van Valen, 1978

**Holotype**—AMNH 2377, right M2.

**Diagnosis**—Differs from *D. hermaeus* and *D. mearae* in being smaller; also differs from *D. protogonoides* in having a better-developed upper molar hypocone.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

#### *Deuterogonodon montanus* Gidley in Simpson, 1935

Fig. 14

**Holotype**—USNM 6061, right maxillary fragment with M3 and fragments of M1-2.

**Diagnosis**—The M1 and M3 hypocones are vestigial; the hypocone is better developed on the M2. The upper molar cingulum is well developed, and the mesostyle is usually present (at least on the M1). The parastyle is very large. Lower molar trigonid is taller than the talonid, the metaconid is smaller than the protoconid, the paraconid is reduced and median in position.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico and Montana.

**Comments**—Williamson (1996) pointed out that the difference between *D. montanus* and *D. "noletil"* is insignificant and cannot be used to differentiate the two species. The two species were not synonymized because of lack of specimens of *D. montanus*. However, the development of a mesostyle and slightly smaller size of *D. "noletil"* cannot be used to differentiate the two species, so we consider the latter to be a junior subjective synonym of *D. montanus*.

Van Valen (1978, 1988) suggested that *Deuterogonodon* is an ancestor of Dinocerata based on the comparison of *Deuterogonodon*, *Prodinoceras* and *Carodnia*. Lucas (1993) noted that characters used by Van Valen were insignificant because of existing morphological variability of the *Deuterogonodon* dentition.

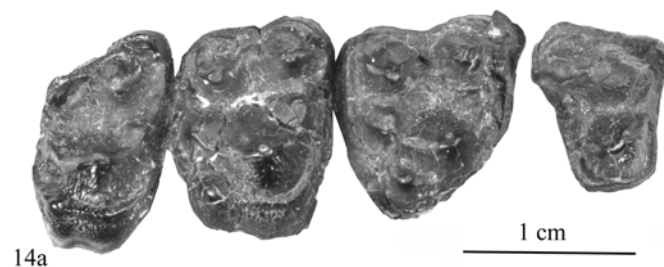


FIGURE 14. *Deuterogonodon montanus*, AMNH 17078, right P4-M3 (holotype of *Deuterogonodon "noletil"*), occlusal view (a).

#### ORDER CONDYLARTHRA COPE, 1881

##### Suborder Taligrada Cope, 1881

##### Family Periptychidae Cope, 1882

##### Subfamily Periptychinae Cope, 1882

##### *Periptychus carinidens* Cope, 1881

**Holotype**—AMNH 3620, dentary fragments with dp3-4.

**Diagnosis**—Differs from *P. coarctatus* in having more laterally compressed posterior upper premolars and molars, a relatively larger paraconid and metaconid on the lower premolars, and protoconid and metaconid connected by a crest. Also differs from *P. coarctatus* in having a more complex talonid structure: the cristid obliqua begins from a small metaconulid, runs posteriorly and bifurcates before reaching the hypoconulid.

**Distribution**—Lower Paleocene (Torrejonian) of North America.

**Comment**—*P. rhabdodon* and *P. superstes* are junior subjective synonyms of *P. carinidens*. Specimens from Big Bend, Texas, that Schiebout (1974) referred to *P. superstes* are much larger than typical *P. carinidens* and do not possess the characteristics of *P. "superstes,"* such

as an enlarged m3 talonid. Therefore, it belongs to a new species of *Periptychus*. Similar large *Periptychus* was reported from the Animas Formation (Tiffanian) of Colorado (Burger, 2004), which may be conspecific with the Texas *Periptychus*.

***Periptychus coarctatus* Cope, 1883**

**Holotype**—AMNH 3775, isolated left c, p3, p4 and m1.

**Diagnosis**—A species of *Periptychus* that has the posterior premolars and molars relatively wider than in *P. carinidens*, has a relatively smaller paraconid and metaconid that are not connected by a crest and has a relatively simple structure of the talonid basin.

**Distribution**—Lower Paleocene (Puercan) of North America.

**Comment**—Van Valen (1978) suggested that *P. matthewi* is a subjective junior synonym of *P. coarctatus*, which was supported by Williamson (1996), and we concur. Also see the discussion of the generic status of *Periptychus coarctatus* in Williamson (1996).

***Ectoconus ditrigonus* (Cope, 1882)**

**Holotype**—AMNH 3798, right dentary fragment with m2.

**Diagnosis**—Large species of *Ectoconus* that differs from *E. symbolus* by its larger size (15-40%) and presence of the p4 paraconid.

**Distribution**—Lower Paleocene (Puercan) of New Mexico, Colorado, Utah and Wyoming.

**Subfamily Anisonchinae Osborn et Earle, 1895**

***Anisonchus sectorius* (Cope, 1881)**

**Holotype**—AMNH 3527, associated right maxillary fragment with P2-M2 and right dentary with p2-m2

**Diagnosis**—Differs from *A. athelas* in having square M1-2 and in lacking the anterior cingulum on upper molars. Differs from *A. willeyi* in having equally developed paracone and metacone on M2 and in having a small hypocone, which is directly posterior to the protocone. Differs from *A. oligistus* in having square M1-2, lacking the pericone on the upper molars and having the m1 trigonid wider than the talonid. Differs from *A. fortunatus* in having square M1-2, lacking the pericone on the upper molars and in the position of the hypocone, which has a base that is not shifted lingually; also differs in having equally developed M1-2 paracone and metacone.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico and Utah.

**Comment**—Williamson (1996) suggested that *A. dracus* is a junior subjective synonym of *A. sectorius*. Considering that the two species are very close in morphology and do not differ in size, we concur.

***Anisonchus gillianus* (Cope, 1882)**

**Holotype**—AMNH 3543, left maxillary fragment with P2-M2, left dentary fragment with p2-m3 and postcranial fragments.

**Diagnosis**—Differs from other *Anisonchus* species in having closely grouped trigonid cuspids; talonids relatively more robust. Upper molars relatively wider than in other species of *Anisonchus* and the premolars are more triangular. Differs from *Earendil* in having weak anterior cingulum on upper molars, well-developed hypocone and lacking the ectoflexus on upper molars.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—Rigby (1981) placed *Anisonchus gillianus* in a new genus *Gillisonchus*. “*Gillisonchus*” *gillianus* is very similar to the representatives of the genus *Anisonchus*, so we return it to *Anisonchus*. Morphological distance between “*Gillisonchus*” *gillianus* and the type species of *Anisonchus* (*A. sectorius*) is not greater than morphological distances between the known species of *Anisonchus*.

***Haploconus angustus* (Cope, 1881)**

**Holotype**—AMNH 3477, right dentary fragment with p4-m3.

**Diagnosis**—Upper premolars robust, molars trapezoidal, with a small pericone and a well-developed hypocone. Mesostyle is not developed. Cusps of trigon and cuspids of trigonid are closely grouped. Hypoconulid is always developed. Differs from *Hemithlaeus* species in having greatly reduced lower molar paraconids, in lacking a mesostyle on the upper molars and in having a relatively small pericone.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comments**—Simpson (1959) noted that *H. angustus*, *H. inopinatus* and *H. corniculatus* are very close in morphology. Williamson (1996) suggested that *H. inopinatus* and *H. corniculatus* are junior subjective synonyms of *H. angustus*, and we concur.

***Hemithlaeus kowalewskianus* Cope, 1882**

**Fig. 15**

**Holotype**—AMNH 3587, right dentary fragment with p2-m2, left dentary fragments with p1-2, and m1-2.

**Diagnosis**—Upper molars are very wide, enamel is not wrinkled and pericone is well-developed. Paraconule and metaconule are present, as well as a small, but distinct mesostyle. Paraconid of lower molars is considerably reduced, but always present. Differs from *H. josephi* in having a larger pericone.

**Distribution**—Lower Paleocene (Puercan) of New Mexico and Montana.

**Comments**—Archibald (1998) placed *Hemithlaeus* in the subfamily Periptychinae, but noted significant distance between this genus and the other periptychines. However, *Hemithlaeus* does not possess the advanced features of this subfamily and should be referred to Anisonchinae.

Van Valen (1978) described a new genus *Tinuviel* with a single species *T. eurydice* and used characters such as large pericone and unreduced paraconid to differentiate *Tinuviel* from other periptychids. These characters are typical of *Hemithlaeus*. Considering the very similar morphology and close size of *Hemithlaeus kowalewskianus* and *Tinuviel eurydice*, we suggest that the latter is a junior subjective synonym of the former, and that *Tinuviel* is a junior subjective synonym of *Hemithlaeus*.

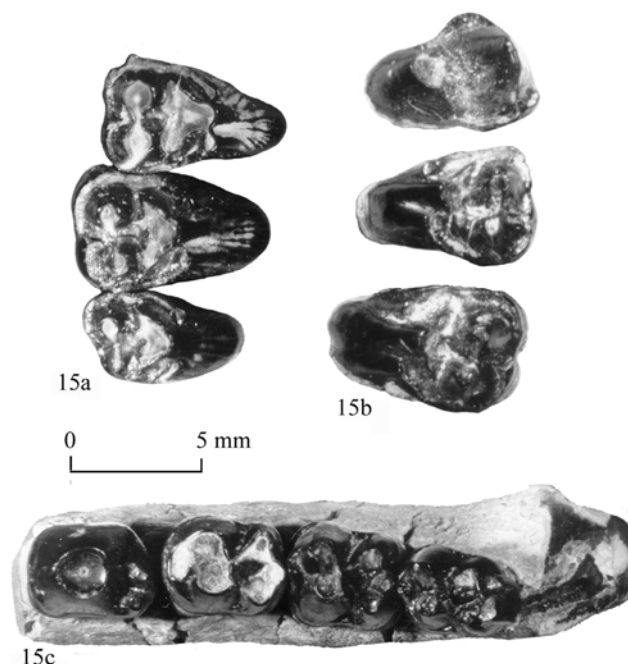


FIGURE 15. *Hemithlaeus kowalewskianus*, NMMNH 8828, right M1-3, occlusal view (a); NMMNH 8680, left P4-M2, occlusal view (b); NMMNH 15044, right dentary fragment with p4-m3.



*Conacodon entoconus* (Cope, 1882)

## Fig. 16

**Holotype**—AMNH 3462, right dentary fragment with p3-m3.

**Diagnosis**—Differs from *C. kohlbergi* in being significantly larger (30%), in having a less developed upper molar metacone and in lacking the parastyle on the P4. Differs from *C. cophater* in lacking the parastyle on the  $\overline{D}4$ .

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

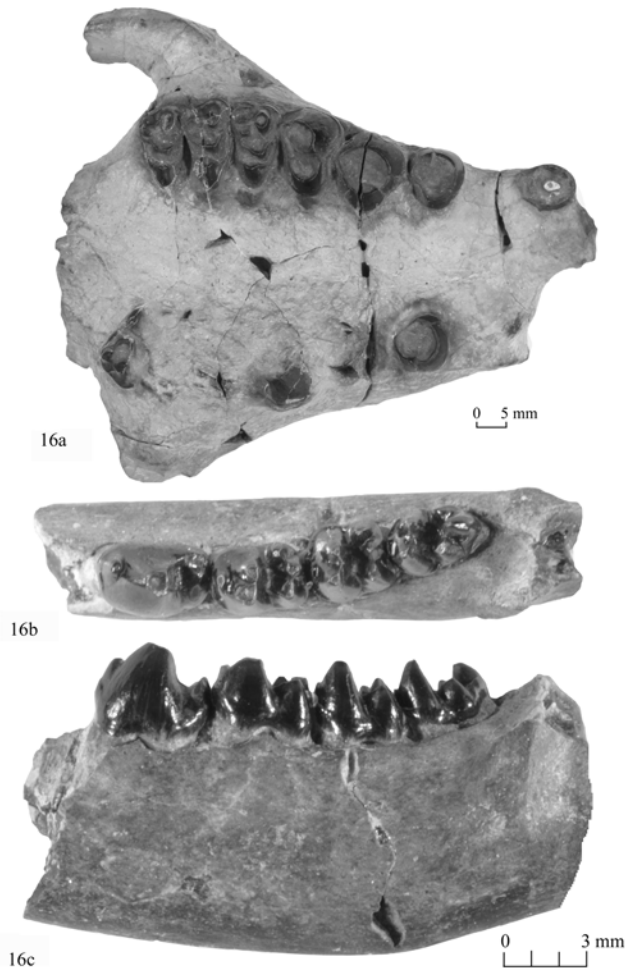


FIGURE 16. *Conacodon entoconus*, KUPV 1310, skull fragment with right P2-M2 and left P2, ventral view (a); NMMNH 21865, left dentary fragment with p4-m3.

*Conacodon cophater* (Cope, 1884)

**Holotype**—AMNH 3486, a skull fragment with left P4-M2 and right P3-M3.

**Diagnosis**—Differs from *C. kohlbergi* in being larger (20-30%). Differs from *C. entoconus* in having a well-developed P4 parastyle and slightly smaller size.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—Matthew (1897, 1937) referred *Anisonchus cophater* Cope, 1884 to *Conacodon*. Van Valen (1978) argued that this species is closer to the genus *Oxyacodon*. Archibald (1982) and Archibald et al. (1983b) demonstrated that “*Anisonchus*” *cophater* belongs to the genus *Conacodon*.

*Conacodon kohlbergi* Archibald, Schoch and Rigby, 1983

**Holotype**—NMMNH 27707 (originally described under catalogue number UNM B1700), palate with right P4-M2, left P3-M2,

isolated right P2, bone fragment with right P3, right dentary with p4-m3, left dentary with p3-m1 and isolated right p2.

**Diagnosis**—Differs from *C. entoconus* and *C. cophater* in being smaller (20-30%); also differs from the former in having a well-developed upper molar metaconules and P4 parastyles.

**Distribution**—Lower Paleocene (Puercan) of New Mexico and Utah.

**Comment**—Robison (1986) described *C. utahensis* from Utah and compared the new species with *C. entoconus* and *C. cophater* but not with *C. kohlbergi*. Williamson (1996) pointed out that *C. utahensis* is a junior subjective synonym of *C. kohlbergi*. Both species are very close in size and in morphology, so we concur.

*Oxyacodon apiculatus* Osborn and Earle, 1895

**Holotype**—AMNH 816, damaged left dentary fragment with p4-m2.

**Diagnosis**—Differs from *O. agapetillus* in being slightly larger (15-20%) and in having different M1/P4 and m1/p4 ratios, where the M1 is almost the same length as the P4 and the m1 length is close to that of the p4. Differs from *O. priscilla* in being slightly larger (15-20%), in having an ectoflexus on the upper molars, reduced M3 metacone and large M3 parastyle.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—Van Valen (1978) described *O. marshater* based on an isolated m2 with the following diagnosis: “m2 transverse, paraconid a small cusp, metacristid present, entoconid as large as relatively large hypoconulid.” Archibald et al. (1983a) noted that the validity of this species is dubious, but the large size (comparable to *O. apiculatus*) may prove its validity. *O. marshater* is indeed larger than *O. priscilla* but does not differ significantly in size from *O. apiculatus*. Such morphological features as enlarged entoconid and vestigial metacristid are found in both *O. marshater* and *O. apiculatus*, so they are conspecific, and *O. marshater* is a junior subjective synonym of *O. apiculatus*.

*Oxyacodon agapetillus* (Cope, 1884)

**Lectotype**—AMNH 3557, dentary fragment with m1-2.

**Diagnosis**—Differs from *O. apiculatus* in being slightly smaller (15-20%) and in having a different M1/P4 to m1/p4 ratio, where the M1 is longer and wider than the P4 and the m1 is longer than the p4. Differs from *O. priscilla* in having an ectoflexus on upper molars, reduced M3 metacone and large M3 parastyle.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—Matthew (1937) designated two dentary fragments as the holotype of this species. Van Valen (1978) restricted the holotype to one fragment and described a new genus and species, *Fimbrethil ambaronae*, based on the other one. Archibald et al. (1983a) demonstrated that the two specimens belong to one species and synonymized *Fimbrethil ambaronae* with *Oxyacodon agapetillus*, but retained one specimen as a holotype for the latter species (AMNH 3557).

*Oxyacodon priscilla* Matthew, 1937

## Fig. 17

**Holotype**—AMNH 3547, right dentary fragment with p2-m3.

**Diagnosis**—Differs from *O. apiculatus* in being slightly smaller (15-25%), in lacking the upper molar ectoflexus and in having an unreduced M3 metacone; also differs in the M1/P4 ratio, where the M1 is longer and wider than the P4. Differs from *O. agapetillus* in lacking the upper molar ectoflexus, in having an unreduced M3 metacone, and a weak M3 parastyle.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—Van Valen (1978) suggested that *O. priscilla* and *Escatepos campi* are junior synonyms of *O. agapetillus*. Archibald et al. (1983a) argued that *O. priscilla* is a distinct species. They also described *O. ferronensis*, which is almost identical to *O. priscilla* in both size and

morphology. The only character that differentiates the two species is the length ratio between M1 and M2. This difference is only 2-3%, which may be due to intraspecific variation and does not warrant specific separation. In such features as lack of the ectoflexus on the upper molars and hypocone position, "*O. ferronensis*" is identical to *O. priscilla*, so we consider them synonymous.

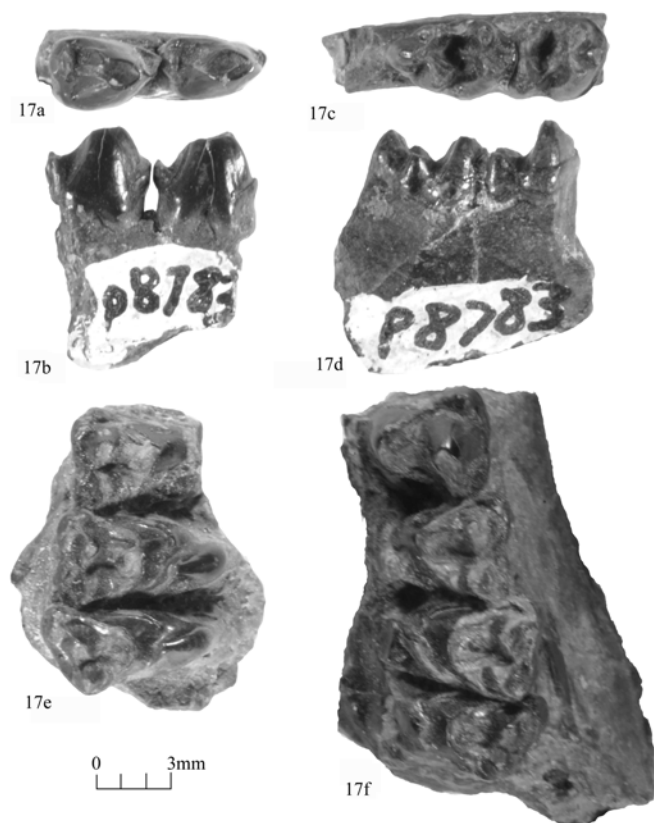


FIGURE 17. *Oxyacodon priscilla*, NMMNH 8783, right dentary fragment with p2-3, occlusal (a) and labial (b) views; right dentary fragment with m2-3, occlusal (c) and labial (d) views; right maxillary fragment with M1-3, occlusal view (e); left maxillary fragment with P4-M3, occlusal view (f).

#### Suborder Phenacodonta McKenna, 1975

#### Superfamily Hyopsodontioidea Trouessart, 1879

#### Family Hyopsodontidae Trouessart, 1879

#### Subfamily Hyopsodontinae Trouessart, 1879

#### *Litomylos osceolae* Van Valen, 1978

**Holotype**—AMNH 16039, left dentary fragment with m1-3.

**Diagnosis**—Molars relatively and absolutely more elongate than in *L. dissentaneus*; m3 is much more elongate and the m2 talonid basin is open. Differs from *L. dissentaneus* in having rhomboid-shaped talonid basins.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico and Wyoming.

**Comment**—Rigby (1980) noted that the size differences between *L. osceolae* and *L. dissentaneus* are insignificant. Williamson (1996) pointed out that a rounded anterior margin of the p4 cannot be used to differentiate these two species and suggested that *L. osceoli* is a junior subjective synonym of *L. dissentaneus*. The difference in size is indeed minute, but the shape of the lower molars and especially of the m3 differs significantly in these two species, so we consider *L. osceoli* a valid species.

#### Superfamily Mioclaenoidea Osborn et Earle, 1895

#### Family Mioclaenidae Osborn et Earle, 1895

#### Subfamily Mioclaeninae Osborn et Earle, 1895

#### *Mioclaenus turgidus* Cope, 1881

#### Fig. 18

**Holotype**—AMNH 3135, dentary fragments with left p4-m2, right p4-m1 and left maxillary fragment with P4-M2.

**Diagnosis**—Lower molar paraconids completely reduced, M3 and m3 extremely reduced and premolars inflated.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

**Comment**—One of the most advanced mioclaenids known.



FIGURE 18. *Mioclaenus turgidus*, NMMNH 18846, right dentary fragment with p3-m2, occlusal (a) and labial (b) views.

#### *Choeroclaenus turgidunculus* (Cope, 1888)

#### Fig. 19

**Holotype**—AMNH 3291, maxillary fragment with P4-M2.

**Diagnosis**—Differs from *Litaletes* species in having reduced lower molar paraconids that are pressed onto the metaconids. Differs from *Mioclaenus turgidus* in retaining lower molar paraconids and less reduced M3/m3. Differs from *Promioclaenus* and *Ellipsodon* species in having differentiated entoconids and hypoconulids on m1-2. Differs from *Tiznatzinia prisca* in having closed talonid basins of lower molars.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

#### *Ellipsodon inaequidens* (Cope, 1884)

**Holotype**—AMNH 3095, skull fragments with left P2-3, M1-3 and right P4, M2-3.

**Diagnosis**—Differs from *E. grangeri* in its smaller size (20%) and in having a weak lower molar precingulid that does not form additional cusps.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

#### *Ellipsodon grangeri* Wilson, 1956

#### Fig. 20

**Holotype**—KUPV 7833, mandibular fragments with right m1-3 and left m3.

**Diagnosis**—Differs from *E. inaequidens* in being larger and in having a strong lower molar precingulid that often forms additional cusps.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

**Comment**—Our attempt to locate the holotype in the KUPV collection was unsuccessful.

#### *Promioclaenus acolytus* (Cope, 1882)

#### Fig. 21



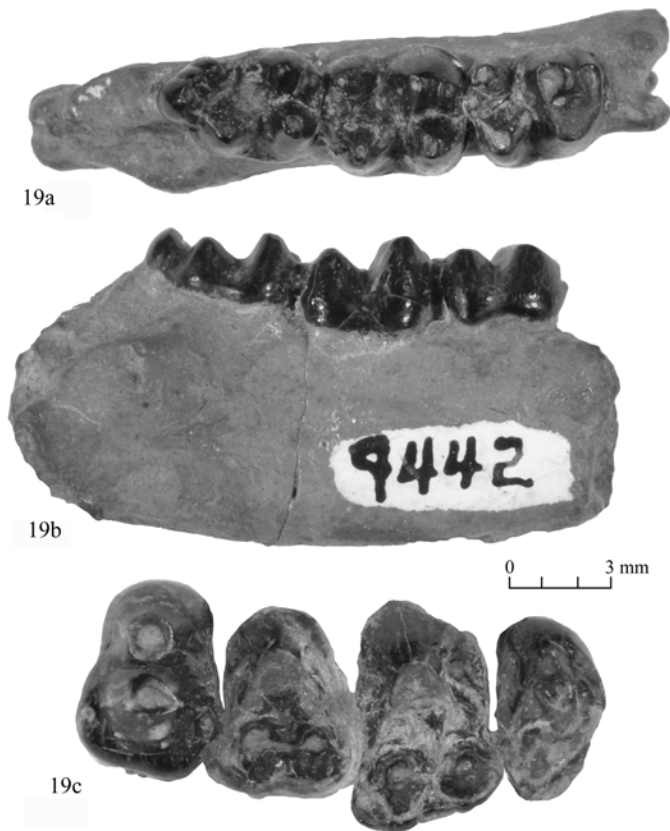


FIGURE 19. *Choeroclaenus turgidunculus*, KUV 9442, right mandibular fragment with m1-3, occlusal (a) and labial (b) views; KUV 9444, right P4-M3, occlusal view (c).

**Holotype**—AMNH 3208, left maxillary fragment with P3-M2 and left dentary fragment with p3-m3.

**Diagnosis**—Differs from *P. lemuroides* and *P. pipiringosi* in being 20% smaller; differs from *P. wilsoni* in having a less molarized p4 that does not have a metaconid.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

**Comment**—Rigby (1980) demonstrated that *Ellipsodon aquilonius* Simpson, 1935, which Wilson (1956) referred to *Promioclænus*, is a junior subjective synonym of *P. acolytus*.

***Promioclænus lemuroides* (Matthew, 1897)**

Fig. 22

**Holotype**—AMNH 16403, mandibular fragments with left p2-m3 and right p4-m2.

**Diagnosis**—The incisors are small and the canine is larger, about the size of the p1. The p1 is single-rooted and the other lower premolars are double-rooted. The molars are simple and flattened and the talonid basin is shallow. Differs from *P. acolytus* in being 20% larger; differs from *P. pipiringosi* in having more flattened premolars. Differs from *P. wilsoni* in having a less molarized p4 that does not have a metaconid.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

***Promioclænus wilsoni* Van Valen, 1978**

**Holotype**—KUV 9446, skull fragment with left P4-M3 and right P3-M2, right dentary fragment with p1, p3-m2, left dentary fragment with p2-3.

**Diagnosis**—Teeth are less flattened than in other species of the genus and the posterior cingulum of the upper molars is interrupted by a labial cingulum. The p4 has a distinct metaconid and tall paraconid that is situated close to the protoconid.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

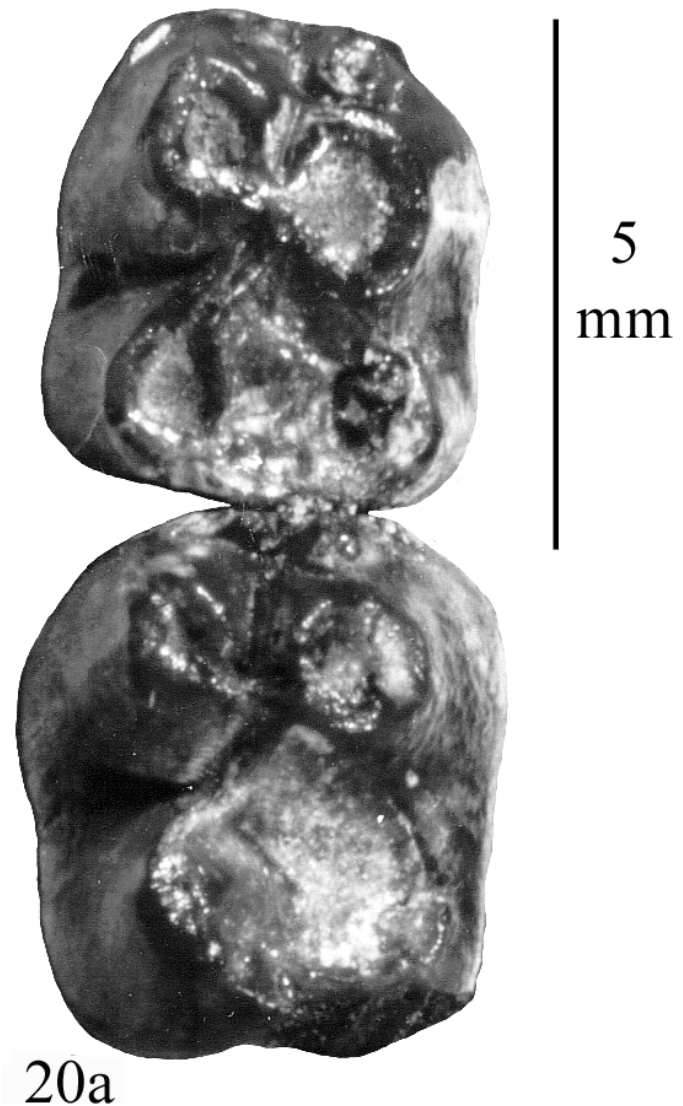


FIGURE 20. *Ellipsodon grangeri*, NMMNH 15852, left m1-2, occlusal view (a).

***Tiznatzinia vanderhoofi* Simpson, 1936**

**Holotype**—UCMP-31264, left dentary with p4-m2.

**Diagnosis**—Lower molar paraconids somewhat reduced, but always present. P4/p4 are elongate. The talonid basins of the lower molars are open. Differs from *Litaletes* species in having slightly reduced paraconids. Differs from *M. turgidus* in having less reduced M3/m3 and lower molar paraconids. Differs from *Ch. turgidunculus* in having open lower molar talonid basins. Differs from *T. prisca* in its much smaller size, more laterally compressed p4 and narrower lower molars.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

***Tiznatzinia prisca* (Matthew, 1937)**

**Holotype**—AMNH 16403, left dentary fragment with p2-m3 and right dentary fragment with p3-m3.

**Diagnosis**—The m3 is slightly reduced and m1-3 are very short and wide. The paraconids are distinct on all the lower molars. Differs from *T. vanderhoofi* in being significantly larger and in having a wider p4 and m1-2. The paraconid is more reduced than in *T. vanderhoofi*.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—Simpson (1936) referred three species to his new genus *Tiznatzinia*: *T. vanderhoofi*, "*Mioclænus*" *turgidunculus* and

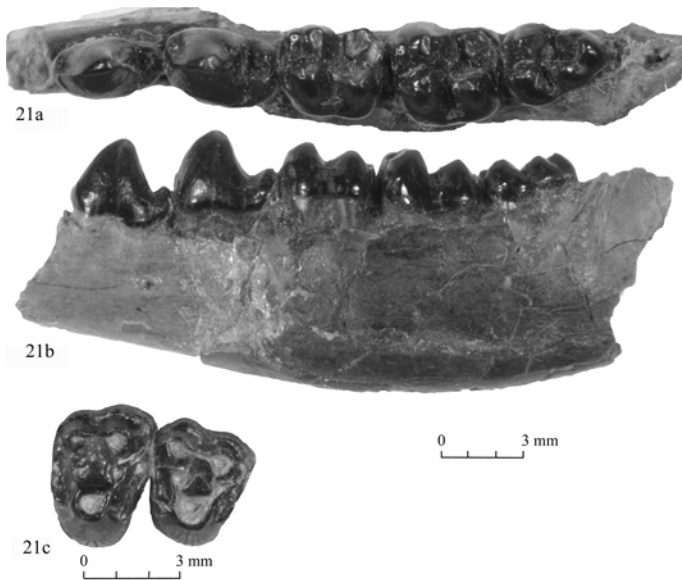


FIGURE 21. *Promioclæmus acolytus*, KUV 9626, left dentary fragment with p3-m3, occlusal (a) and labial (b) views; KUV 9623, right maxillary fragment with M1-2, occlusal view (c).

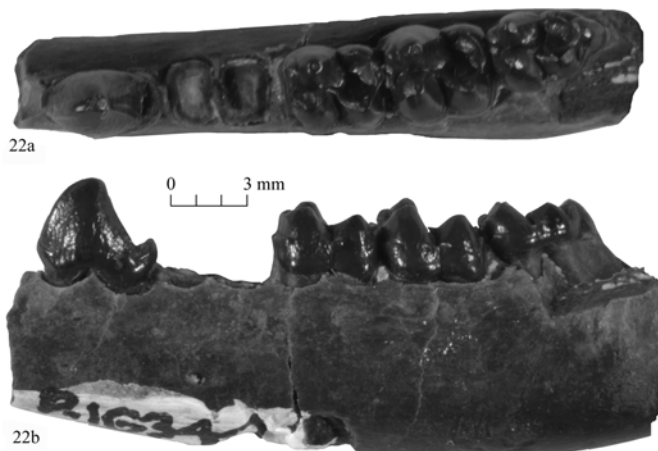


FIGURE 22. *Promioclæmus lemuroides*, NMMNH 16349, left mandibular fragment with p4, m1-3, occlusal (a) and labial (b) views.

"*Ellipsodon*" *priscus*. Later, "*Mioclæmus*" *turgidunculus* was referred to a new genus *Choeroclæmus* (Simpson, 1937). Van Valen (1978) synonymized *Tiznatzinia* with *Promioclæmus* and referred "*Ellipsodon*" *priscus* to a new genus, *Bomburia*. Cifelli (1983) resurrected the genus *Tiznatzinia* with a single species *T. vanderhoofi*, synonymized *Bomburia* with *Ellipsodon* and placed "*Bomburia*" *prisca* back in *Ellipsodon*. Williamson (1996) insisted on retaining the genus *Bomburia* based on the more archaic morphology of "*Bomburia*" *prisca* compared to *Ellipsodon* species. In the original diagnosis of *Tiznatzinia*, Simpson (1936) indicated that species of this genus are more primitive than the species of *Ellipsodon*. The morphology of "*Bomburia*" *prisca* fits the diagnosis of the genus *Tiznatzinia* well, so we suggest that "*Ellipsodon*" *priscus* should be placed in *Tiznatzinia* and *Bomburia* is a junior synonym of *Tiznatzinia*.

#### Subfamily Protoseleninae Rigby, 1980

##### *Protoselene opisthacus* (Cope, 1882)

Fig. 23

**Holotype**—AMNH 3275, left dentary with p4-m3, right dentary with m1-3.

**Diagnosis**—The premolars are not flattened and slightly inflated. The P4 has a well-developed protocone and a distinct metacone. The p4 has a well-developed talonid. Differs from *P. bombadili* in larger size and developed mesostyle. Differs from *P. novissimus* in deeper talonid basins, taller crests and more isolated lower molar paraconids. Differs from *P. griphus* in having a well-differentiated P4 protocone.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

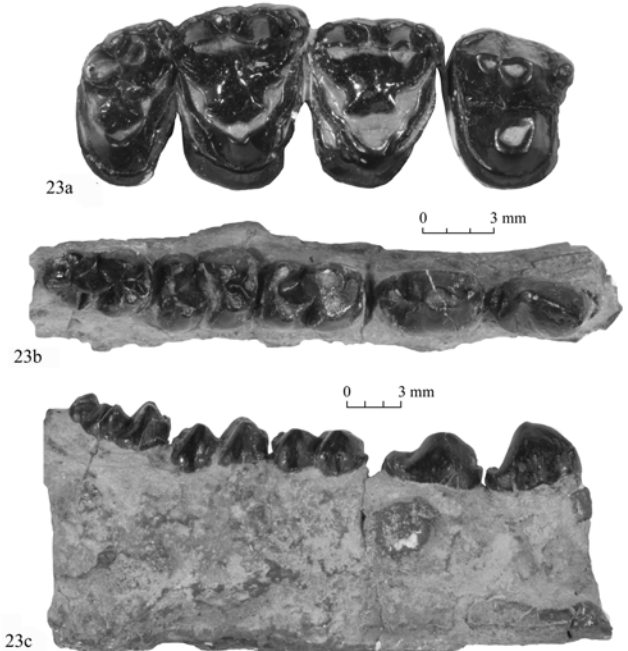


FIGURE 23. *Protoselene opisthacus*, KUV 7851, right maxillary fragment with P4-M3, occlusal view (a); KUV 14007, right dentary fragment with p3-m3, occlusal (b) and labial (c) views.

##### *Protoselene bombadili* Van Valen, 1978

**Holotype**—USNM 23285, left maxillary fragment with M2.

**Diagnosis**—The M2 is rounded, and the cingulum is extremely strong, interrupted at the lingual base of the protocone. There is a small parastyle on the upper molars and the mesostyle is not developed. Differs from other species of *Protoselene* in being much smaller. Differs from *P. opisthacus* in lacking the upper molar hypocones and mesostyles.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

#### Superfamily Phenacodontoidea McKenna, 1975

##### Family Phenacodontidae Cope, 1881

##### Subfamily Phenacodontinae Cope, 1881

##### *Tetraclaenodon puercensis* (Cope, 1881)

Fig. 24

**Holotype**—AMNH 3832, left dentary with m2-3, right dentary with m1-3 and left maxillary fragment with M1-3.

**Diagnosis**—The tooth formula is complete. There are short diastemata between the C/c and P1/p1. P1/p1 simple, with a single cusp, P3/p3 is relatively molarized. M1-2 have six cusps and M3 is somewhat reduced. Lower molars are rectangular in shape. The lower molar paraconid is weak, but distinct. There is an entoconulid on all lower molars. Hypoconulid is large on all lower molars. Differs from *Phenacodus* and *Copecion* species in lacking the mesostyle on upper molars. Differs from *Copecion* species in having shorter premolars.

**Distribution**—Lower Paleocene (Torrejonian) of North America.

**Comment**—There are two size groups of Torrejonian *Tetraclaenodon*—the larger one that includes the type and the group that

includes smaller specimens that were referred to a different species, *T. symbolicus* by Simpson (1935). Thewissen (1990) doubted the validity of the latter species and synonymized it with *T. puercensis*. Williamson (1996) recognized two subspecies of *T. puercensis*: *T. puercensis puercensis* and *T. puercensis pliciferus*. A newly discovered specimen of a very small *Tetraclaenodon* from the San Juan Basin, represented by an almost complete skeleton, is currently under study. We hope that it will

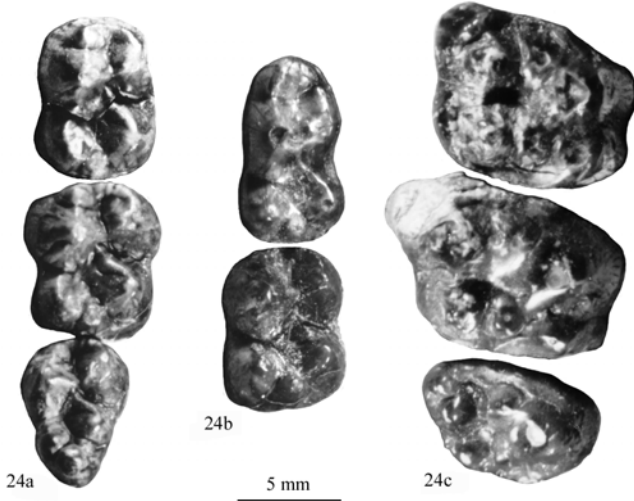


FIGURE 24. *Tetracaelaenodon puercensis*, NMMNH 16136, right m1-3, occlusal view (a); NMMNH 15782, right dp4-m1, occlusal view (b); NMMNH 16221, right M1-3, occlusal view (c).

shed some light on the complex taxonomy of *Tetraclaenodon*.

**Order Acrodi Matthew, 1909**  
**Family Mesonychidae Cope, 1875**  
*Dissacus navajovius* (Cope, 1881)  
**Fig. 25**

**Holotype**—AMNH 3356, mandibular fragments with left p4-m3 and right p3-m3.

**Diagnosis**—Differs from *Ankalagon saurognathus* in its much smaller size.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

*Ankalagon saurognathus* (Matthew, 1897)  
**Fig. 26**

**Holotype**—AMNH 2454, left complete dentary with c, p1-4 and m1-3.

**Diagnosis**—Differs from *Dissacus navajovius* in being much larger.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

**Comment**—The species was originally described as *Dissacus*, but was placed in a new genus by Van Valen (1980).

**Family Triisodontidae Scott, 1892**  
*Triisodon quivirensis* Cope, 1881  
**Fig. 27**

**Holotype**—AMNH 3352, dentary fragments with canines, dp4-m2.

**Diagnosis**—Differs from *T. crassiscuspis* in much larger size. Differs from *Eoconodon* species in having somewhat reduced m3.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

**Comment**—Van Valen (1978) synonymized *Triisodon antiquus* with *T. quivirensis*. Tomida (1981) argued that *T. antiquus* is valid. Williamson (1996) evaluated a larger sample of *Triisodon* and stated that the synonymy was justified, and we concur.

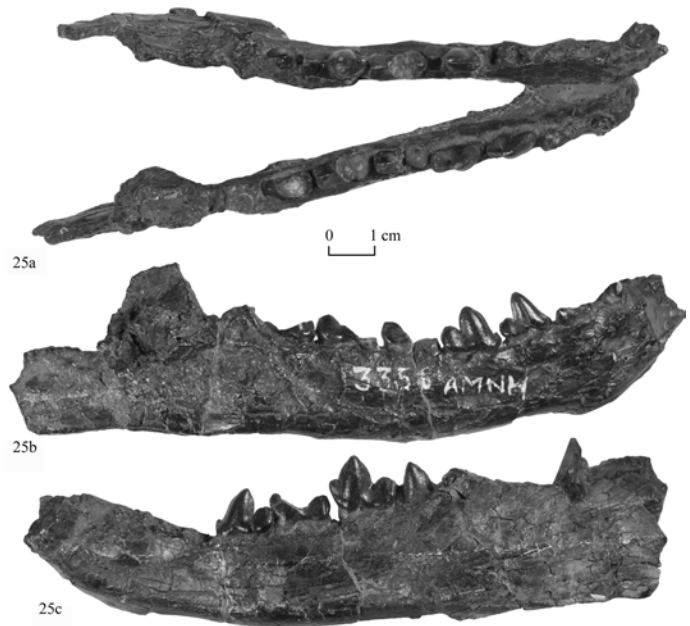


FIGURE 25. *Dissacus navajovius*, AMNH 3356, mandible with left p4-m3 and right p2-m3 (holotype), occlusal (a), right labial (b) and left labial (c) views.



FIGURE 26. *Ankalagon saurognathus*, AMNH 2454, left dentary with c-m3 (holotype), occlusal (a) and labial (b) views; AMNH 776, left P2-M3 and right P3-M3, occlusal view (c).

*Triisodon crassiscuspis* (Cope, 1882)

**Holotype**—AMNH 3178, dentary with m2 talonid and m3.

**Diagnosis**—Differs from *T. quivirensis* in being significantly smaller and in having a more elongate P3. Differs from *Eoconodon* species in having somewhat reduced m3.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

**Comment**—Matthew (1937) referred “*Conoryctes*” *crassiscuspis* Cope, 1882 (= *Triisodon rusticus* Cope, 1884) to *Triisodon*. Van Valen (1978) placed this species in *Goniaconodon* following Scott’s (1892) referral of *T. rusticus* to that genus. Based on a new specimen, Williamson (1996) argued that “*Conoryctes*” *crassiscuspis* belongs to *Triisodon*, and we concur.

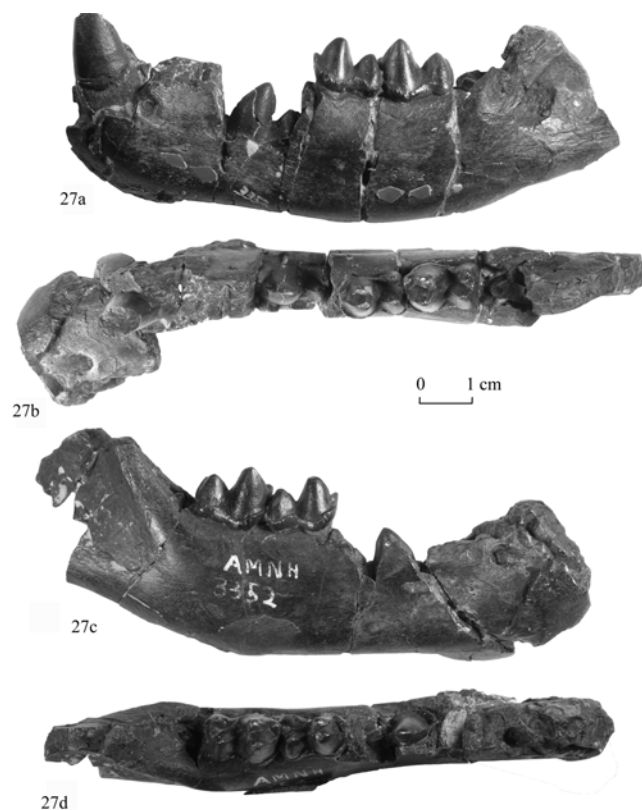


FIGURE 27. *Triisodon quivirensis*, AMNH 3352, right dentary with c, p4-m2, and erupting m3, labial (a) and occlusal (b) views, right dentary with p4-m2, labial (c) and occlusal (d) views.

***Eoconodon gaudrianus* (Cope, 1888)**

**Fig. 28**

**Holotype**—AMNH 3200, dentary and maxillary fragments, calvarium.

**Diagnosis**—Intermediate in size between the other two San Juan Basin species. Differs from *Triisodon* species in having an unreduced m3.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

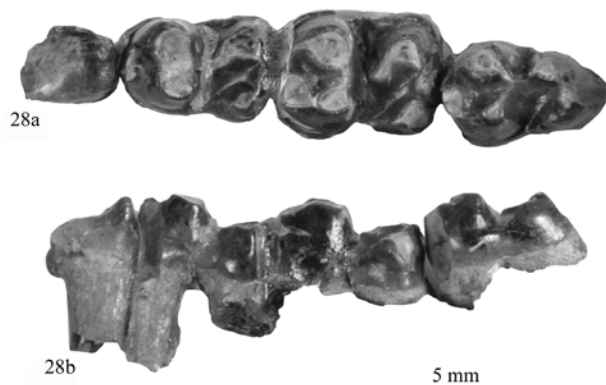


FIGURE 28. *Eoconodon gaudrianus*, AMNH 58116, right p4 talonid, m1-3, occlusal (a) and labial (b) views.

***Eoconodon coryphaeus* (Cope, 1885)**

**Fig. 29**

**Lectotype**—AMNH 3181, incomplete skull.

**Diagnosis**—Largest species of *Eoconodon*. Differs from *Triisodon* species in having an unreduced m3.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—Van Valen (1978) indicated that the holotype of *Triisodon heilprinianus* Cope, 1882 is “an unworn molar referable to the taeniodont *Conoryctes comma*.” Schoch and Lucas (1981) argued that the specimen belongs to *Huerfanodon*. Van Valen (1978) indicated that the next available name is “*Sarcothraustes*” *coryphaeus* and identified the skull (AMNH 3181) as the type specimen.

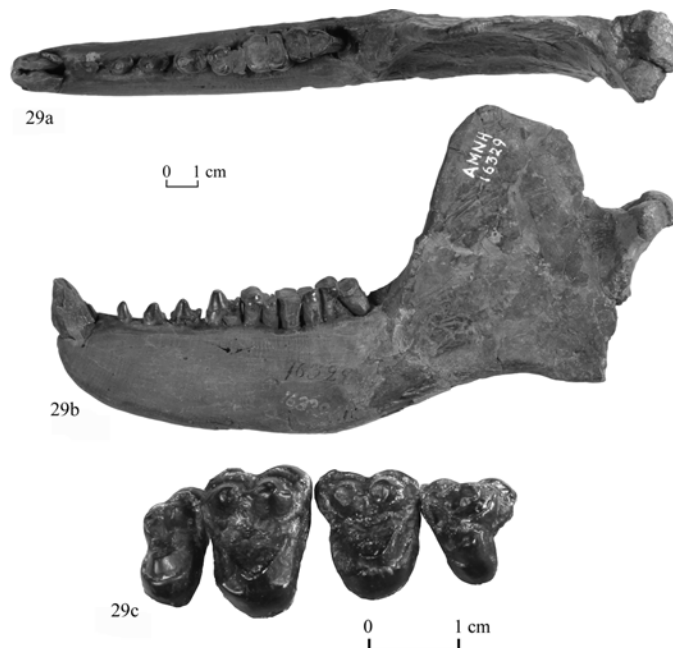


FIGURE 29. *Eoconodon coryphaeus*, AMNH 16329, left dentary with c-m3, occlusal (a) and labial (b) views; AMNH 764, right P4-M3, occlusal view (c).

***Eoconodon ginibitohia* Clemens and Williamson, 2005**

**Holotype**—NMMNH 21622, left dentary fragment with p4, m2-3.

**Diagnosis**—Differs from other species from San Juan Basin in being significantly smaller (Clemens and Williamson, 2005). Differs from *Triisodon* species in having an unreduced m3.

**Distribution**—Lower Paleocene (Puercan) of New Mexico.

**Comment**—The holotype specimen was provisionally identified as *Eoconodon* cf. *E. copanus* (Williamson and Lucas, 1993), and later as *Eoconodon* n. sp. (Williamson, 1996).

***Goniacodon levisanus* (Cope, 1883)**

**Fig. 30**

**Holotype**—AMNH 3217, right dentary fragment with p4 fragment and m1-2.

**Diagnosis**—Differs from *Eoconodon* species in having more triangular upper molars. Differs from *Triisodon* species in having more reduced M3 and in having a deep mandible with large symphysis.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

***Microclaelonodon assurgens* (Cope, 1884)**

**Holotype**—AMNH 3215, left dentary fragment with m1-3.

**Diagnosis**—Differs from other triisodontids in its minute size, gracile lower jaw morphology and less robust dentition.

**Distribution**—Lower Paleocene (Torrejonian) of New Mexico.

**Comment**—Scott (1892) placed *Triisodon assurgens* Cope, 1884 in a new genus, *Microclaelonodon*, which he referred to Triisodontidae.



FIGURE 30. *Goniacion levisanus*, AMNH 3217, right dentary with damaged m1-2, occlusal (a) and labial (b) views.

Matthew (1937) placed this genus in Mesonychidae, noting numerous differences from *Dissacus*. Gingerich (1981) argued against the inclusion of this genus in Mesonychidae. Williamson (1996), following Matthew (1937) and Szalay (1969), placed *M. assurgens* in Mesonychidae. In our opinion *Microclanodon* does not possess the distinctive morphological features of the dentition characteristic of mesonychids with extremely well pronounced shearing surfaces such as those of *Dissacus*. The more bunodont dentition of *Microclanodon* resembles the molars of triisodontids, such as *Eoconodon*. Because of that we tentatively place this species in Triisodontidae.

#### STRATIGRAPHIC DISTRIBUTION OF SAN JUAN BASIN ARCHAIC UNGULATES

The Paleocene mammal biostratigraphy of the San Juan Basin was thoroughly studied by various authors (Williamson and Lucas, 1992, 1993; Williamson, 1996), so we will concentrate on analyzing the distribution of archaic ungulates throughout the Paleocene faunal zones of the San Juan Basin. Wood et al. (1941) introduced the concepts of Puercan and Torrejonian North American land-mammal “ages” (NALMA). These concepts evolved for more than half a century, and the recent understanding of these two biochronological units and a brief history can be found in Lofgren et al. (2004). The Paleocene Nacimiento Formation of the San Juan Basin includes mammal assemblages that correspond to part of the Puercan and most of the Torrejonian NALMAs.

The Puercan NALMA is usually subdivided into three to five interval zones: Pu0, Pu1, Pu2, Pu3 and Pu4. In the latest revision of NALMAs, Lofgren et al. (2004) recognized three zones: Pu1 (*Protungulatum*/*Ectoconus*), Pu2 (*Ectoconus*/*Taeniolabis taoensis*) and Pu3 (*Taeniolabis taoensis*/*Periptychus carinidens*). Faunas that correspond to two of these zones (Pu2 and Pu3) are present in the San Juan Basin. Both interval zones are recognized by the appearance of archaic ungulate species.

Pu2 (*Ectoconus*/*Taeniolabis taoensis* interval zone) is recognized by the first appearance of the peripitychid genus *Ectoconus*. In general this zone is characterized by the presence of archaic oxycylenine arctocyonids of the genera *Oxycylenus* and *Loxolophus*, archaic anisonchine peripitychids of the genera *Conacodon*, *Oxyacodon* and *Hemithlaeus* and the appearance of the primitive mioclaenids *Tiznatzinia*, *Choeroclaenus* and *Bubogonia*.

Pu3 (*Taeniolabis taoensis*/*Periptychus carinidens* interval zone) is recognized as an interval between the first appearance of the multituberculate *Taeniolabis taoensis* and the first appearance of the archaic ungulate *Periptychus carinidens*, which is an index fossil of the Torrejonian NALMA. Although very similar in faunal composition to

Pu2, Pu3 is characterized by the wider diversity of oxycylenine arctocyonids and triisodontids of the genus *Eoconodon*. A very distinctive change is observed in the archaic ungulate family Peripitychidae. Most of the archaic representatives of the subfamily Anisonchinae are absent from the Pu3 interval zone, while the first *Periptychus* species — *P. coarctatus* — makes its appearance in this zone. There is no change in the mioclaenid faunas between the Pu2 and Pu3 zones.

As expected, there is a significant faunal change between the Puercan and Torrejonian archaic ungulate faunas. The Torrejonian NALMA is traditionally subdivided into three interval zones, To1, To2 and To3, which were redefined by Lofgren et al. (2004) as following: To1 (*Periptychus carinidens*/*Protoselene opisthacus* zone), To2 (*Protoselene opisthacus*/*Mixodectes pungens* zone) and To3 (*Mixodectes pungens*/*Plesiadapis praecursor* zone).

To1 (*Periptychus carinidens*/*Protoselene opisthacus* interval zone) is recognized by the first appearance of the archaic ungulate *Periptychus carinidens*. There are major changes in the archaic ungulate faunas between Pu3 and To1. These changes involve the disappearance of oxycylenid arctocyonids and their replacement by such new genera as *Tricentes* and *Deuterogonodon*. *Periptychus* species change between Pu3-To1, from *P. coarctatus* to *P. carinidens*. Neither *Ectoconus* nor any of the “conacodontine” anisonchines (*Conacodon*, *Oxyacodon*) cross the Puercan-Torrejonian boundary. *Anisonchus sectorius* replaces *A. gillmanus* in the Torrejonian faunas of the San Juan Basin. The diversity of Mioclaenidae changes dramatically in the Torrejonian with the extinction of three genera (*Bubogonia*, *Choeroclaenus* and *Tiznatzinia*) and appearance of two new genera, *Mioclaenus* and *Promioclaenus*. The first phenacodontid, *Tetraclaenodon puercensis*, makes its appearance in To1 and persists throughout the Torrejonian NALMA.

There are also numerous differences in faunal composition between To1 and To2. They involve mostly appearances of new taxa, rather than extinction of the existing species of archaic ungulates. Generally, To2 (*Protoselene opisthacus*/*Mixodectes pungens* interval zone) is characterized by the extensive radiation of chiacine and arctocyonine arctocyonids that replaced archaic Oxycylenidae in the Torrejonian faunas. Two large species of *Artocyon* co-exist in To2 — *A. ferox* and *A. corrugatus*. *Chriacus* species along with *Tricentes* become some of the most abundant arctocyonids in To2. The only change in the peripitychid family is the appearance of *Haploconus angustus* that is characteristic of this zone. Hyopsodontid condylarths make their first appearance in the San Juan Basin in To2, represented by a single species, *Litomylos osceolae*. Mioclaenids underwent further diversification during To2 with the appearance of five new species: *Protoselene opisthacus*, two species of *Ellipsodon* (*E. inaequidens* and *E. grangeri*) and two species of *Promioclaenus* (*P. acolytus* and *P. wilsoni*). One of the major changes between the To1 and To2 is the appearance of the family Mesonychidae and reappearance of triisodontids in To2, which were absent from To1. Mesonychids are represented by a single large species—*Angalagon saurognathus*. The radiation of triisodontids resulted in the appearance of three new genera, *Triisodon*, *Goniacion* and *Microclanodon*.

The final zone of the Torrejonian in the San Juan Basin is To3 (*Mixodectes pungens*/*Plesiadapis praecursor* interval zone). There are only few differences in the archaic ungulate faunas of To2 and To3. Two more genera of arctocyonids appear in To3 of the San Juan Basin, *Colpoclaenus* and *Prothryptacodon*. Only two genera of peripitychids make it into To3 — *Periptychus carinidens* and *Anisonchus sectorius*. Mioclaenid diversity dwindles to four species. *Triisodon* species do not extend into To3, while the mesonychids are represented by two species in this zone — *Ankalagon saurognathus* and *Dissacus navajovius*.

Archaic ungulates are abundant throughout the Paleocene deposits of the San Juan Basin and can be efficiently used for the biostratigraphy of the region. Several species of archaic ungulates, such as *Ectoconus ditrigonus*, *Periptychus coarctatus*, *Periptychus carinidens*, *Protoselene opisthacus* and several others are index fossils for certain interval zones within the Puercan and Torrejonian NALMAs.

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